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PG Falkowki

Walker O. Smith Jr.
College of William and Mary

H Ducklow
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Temperature effects on export production in the open ocean

Edward A. Laws,[1] Paul G. Falkowski,[2] Walker O. Smith Jr.,[3] Hugh Ducklow,[3] and James J. McCarthy[4]

Abstract. A pelagic food web model was formulated with the goal of developing a quantitative understanding of the relationship between total production, export production, and environmental variables in marine ecosystems. The model assumes that primary production is partitioned through both large and small phytoplankton and that the food web adjusts to changes in the rate of allochthonous nutrient inputs in a way that maximizes stability, i.e., the ability of the system to return to steady state following a perturbation. The results of the modeling exercise indicate that ef ratios, defined as new production/total production = export production/total production, are relatively insensitive to total production rates at temperatures greater than ~25°C and lie in the range 0.1-0.2. At moderate to high total production rates, ef ratios are insensitive to total production and negatively correlated with temperature. The maximum ef ratios are ~0.67 at high rates of production and temperatures of 0°-10°C. At temperatures less than ~20°C, there is a transition from low ef ratios to relatively high ef ratios as total production increases from low to moderate values. This transition accounts for the hyperbolic relationship often presumed to exist between ef ratios and total production. At low rates of production the model predicts a negative correlation between production and ef ratios, a result consistent with data collected at station ALOHA (22°45'N, 158°W) in the North Pacific subtropical gyre. The predictions of the model are in excellent agreement with results reported from the Joint Global Ocean Flux Study (JGOFS) and from other field work. In these studies, there is virtually no correlation between total production and ef ratios, but temperature alone accounts for 86% of the variance in the ef ratios. Model predictions of the absolute and relative abundance of autotrophic and heterotrophic microorganisms are in excellent agreement with data reported from field studies. Combining the ef ratio model with estimates of ocean temperature and photosynthetic rates derived from satellite data indicates that export production on a global scale is ~20% of net photosynthesis. The results of the model have important implications for the impact of climate change on export production, particularly with respect to temperature effects.

1. Introduction

Because of concern over the possible environmental impacts caused by the gradual buildup of CO_2 in the atmosphere, there is growing concern with our imperfect understanding of the role of the ocean in sequestering CO_2 and in particular with the factors that control the transport of fixed carbon into the deep sea [*Azam*, 1998; *Falkowski et al.*, 1998; *Hein and Sand-Jensen*, 1997]. Estimates of net photosynthesis (NP) are available on a global scale based on satellite estimates of chlorophyll concentrations and algorithms developed to describe the relationship between phytoplankton standing crops and photosynthetic rates as a function of surface temperature, solar irradiance, and mixed layer depth [*Bidigare et al.*, 1987; *Longhurst et al.*, 1995; *Antoine et al.*, 1996; *Behrenfeld and Falkowski*, 1997b]. Theoretical physical/biological models based on these and other studies can be used to predict the effect of climatic changes on marine primary production [*Schlitzer*, 1989; *Fasham et al.*, 1990; *Sarmiento et al.*, 1993; *Broecker and Henderson*, 1998; *Geider et al.*, 1998; *McGowan et al.*, 1998].

Although the factors that control net photosynthesis in the ocean have been recognized for many years [*Riley*, 1947], less well understood are the mechanisms that determine the fraction of primary production that is exported from the euphotic zone to the interior of the ocean. In a seminal paper, *Eppley and Peterson* [1979] suggested that there existed a hyperbolic relationship between total primary production and the ratio of new production *sensu Dugdale and Goering* [1967] to total primary production. They designated this ratio f. In a steady state system, new production should balance export production [*Laws*, 1991], and the f ratio should equal the ratio of export production to total primary production. Following *Downs* [1989], we designate this latter ratio the e ratio.

At the present time there is an imperfect understanding of the factors that regulate the e and f ratios. *Platt and Harrison* [1985]

[1] Department of Oceanography, University of Hawaii, Honolulu.
[2] Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey.
[3] Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Point.
[4] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

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suggested that in nitrogen-limited marine waters the f ratio was related to ambient nitrate concentrations in a hyperbolic manner, but *Harrison et al.* [1987] found that in coastal waters the nature of the relationship varied considerably from one location to another. Subsequently, *Platt et al.* [1989, p. 86] concluded that "Elevated new production is a direct consequence of intermittency in the physical forcing of the pelagic ecosystem." *Vézina* [1994, p. 854] examined the relationship between the f ratio and nitrate concentrations during a coastal phytoplankton bloom. He concluded that the f ratio was nonlinearly related to nitrate concentrations at the 50% light level. However, at the 10 and 1% light levels he concluded that "f is not related to NO_3^- concentration but is instead related to variations in the stratification in the NO_3^- profile." Although the Eppley-Peterson model assumes that a positive correlation exists between total primary production and the f ratio, *Karl et al.* [1996] reported a negative correlation between primary production and the e ratio over a period of 3 years at the Hawaiian Ocean Time series (HOT) station (22°45'N, 158°W) in the North Pacific subtropical gyre. *Duarte and Cerbrián* [1996] related the carbon storage/NP ratio in different marine ecosystems to the nature of the autotrophs, including oceanic and coastal phytoplankton, coral reef algae, macroalgae, marsh plants, and mangroves. Expanding on such work, *Rivkin et al.* [1996] examined the relationship between export production and food web structure in the ocean. Rivkin et al. [1996, p. 1166] concluded that "BC [biogenic carbon] export can be independent of the trophic mode of the plankton, and neither food web structure nor observation scale estimates of NP can be used to predict the magnitude or pattern of BC export from the ocean surface."

From 1989 through 1995/1996 the National Science Foundation (NSF) provided funding for a series of field experiments as a part of the Joint Global Ocean Flux Study (JGOFS). A major goal of the experiments was to provide information that would help elucidate the mechanisms and processes that regulate export production and the e ratio. The field experiments included studies conducted during the spring bloom in the North Atlantic (1989), in the Pacific equatorial upwelling system during both El Niño (February-April, 92) and normal upwelling (August-October, 1992) conditions, in the Arabian Sea during both the Northeast (January 1995) and Southwest (July-August 1995) monsoon seasons, and in the Ross Sea during the 1994/1995 and 1995/1996 austral summer. In addition, the NSF/JGOFS program has been funding studies since 1989 at two long-term monitoring sites, one near Bermuda (Bermuda Atlantic Time-series Study (BATS)) and one ~100 km north of the island of Oahu in the Hawaiian Islands (station ALOHA). Recently, the NSF began funding a number of data analysis and theoretical studies as a part of the JGOFS Synthesis and Modeling Program (SMP). A stated objective of the SMP is to utilize results from the JGOFS process and time series studies to develop models that [*Sarmiento and Armstrong*, 1997, p. 26] "capture the essence of carbon cycle processes compactly enough to be usable in large-scale models." The model described here was developed with this goal in mind.

2. Methods

The model employed in this study is shown diagrammatically in Figure 1. Symbols are defined in Table 1. The concentrations and rates are assumed to represent averages within the euphotic

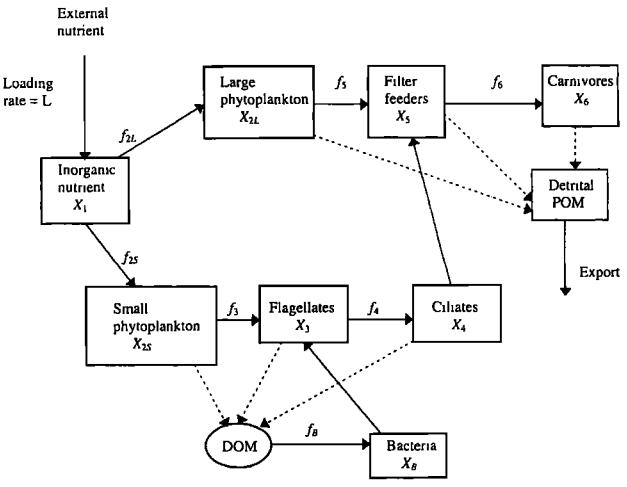

Figure 1. Feeding and excretion relationships in a model pelagic food web in which photosynthetic production is partitioned between small and large phytoplankton cells.

zone. The model assumes that photosynthetic production is partitioned into two food chains, one of which includes only large phytoplankton cells (X_{2L}) and the other of which includes only small phytoplankton cells (X_{2S}). A similar partitioning of primary production is found in models by *Rivkin et al.* [1996] and *Fasham et al.* [1998]. The organisms in the large-cell-based food chain produce detrital particulate organic matter (POM) but no dissolved organic matter (DOM). The small phytoplankton, flagellates, and ciliates in the small-cell-based food chain produce DOM but no detrital POM. The two food chains merge at trophic level X_5, which consists of filter feeders that prey on ciliates and large phytoplankton. The differential equations describing the dynamics of the system are as follows:

$$\frac{dX_1}{dt} = L - (1-r_{2L})F_{2L} - (1-r_{2S})F_{2S} + r_3F_3 + r_4F_4 + r_5F_5 + r_6F_6 + r_BF_B \quad (1)$$

$$\frac{dX_{2S}}{dt} = q_{2S}F_{2S} - F_3\frac{X_{2S}}{X_{2S}+X_B} \quad (2)$$

$$\frac{dX_{2L}}{dt} = q_{2L}F_{2L} - F_5\frac{X_{2L}}{X_{2L}+X_4} \quad (3)$$

$$\frac{dX_3}{dt} = q_3F_3 - F_4 \quad (4)$$

$$\frac{dX_4}{dt} = q_4F_4 - F_5\frac{X_4}{X_{2L}+X_4} \quad (5)$$

$$\frac{dX_5}{dt} = q_5F_5 - F_6 \quad (6)$$

$$\frac{dX_6}{dt} = q_6F_6 - MX_6 \quad (7)$$

$$\frac{dDOM}{dt} = s_{2S}F_{2S} + s_3F_3 + s_4F_4 - F_B \quad (8)$$

Table 1. Definition of Symbols Used in Figure 1 and Equations (1)-(10)

Symbol	Definition
L	External loading rate of limiting nutrient
X_1	Concentration of inorganic nutrient
X_{2S}	Concentration of small phytoplankton
X_{2L}	Concentration of large phytoplankton
X_3	Flagellate concentration
X_4	Ciliate concentration
X_5	Concentration of filter feeders
X_6	Carnivore concentration
DOM	Dissolved organic matter
POM	Detrital particulate organic matter
X_B	Concentration of bacteria
f_m	Rate of uptake or ingestion by X_m
q_m	Fraction of ingested nutrient converted to biomass by X_m
r_m	Fraction of ingested nutrient respired by X_m
s_m	Fraction of ingested nutrient converted to DOM or detrital POM by X_m
D	Fractional loss rate of detrital POM
M	Mortality rate of X_6
A_m	Prey/nutrient-saturated grazing/uptake rate by X_m
P_m	Threshold concentration for grazing/uptake on X_m

$$\frac{dPOM}{dt} = s_{2L}F_{2L} + s_5F_5 + s_6F_6 + MX_6 - D\,POM \quad (9)$$

$$\frac{dX_B}{dt} = q_BF_B - F_3\frac{X_B}{X_{2S} + X_B} \quad . \quad (10)$$

The q_m are gross growth efficiencies, and $q_m + r_m + s_m = 1$. In this analysis we will assume that the system is in steady state, in which case (1)-(10) all equal zero. Under those conditions it is straightforward to show that $L = D$ POM. Determining the steady state values of the other nine state variables requires specification of the ingestion or feeding rates, F_m. We assumed the F_m to take the form

$$F_m = A_mX_m\frac{X_{m-1} - P_m}{X_{m-1}} = A_mX_mf_m\,; \quad (11)$$

where A_m is the prey- or nutrient-saturated grazing/uptake rate by X_m, P_m is the concentration of X_{m-1} at which grazing/uptake of X_{m-1} ceases, and f_m is the growth rate of X_m expressed as a fraction of its substrate- or prey-saturated growth rate. Grazing/uptake of X_{m-1} is 50% of its maximum rate when $X_{m-1} = 2P_m$. With this formulation for the F_m, the steady state values of all the state variables can be determined with matrix algebra. A copy of the computer program that solves the steady state equations is available from the senior author upon request.

Table 2 lists values assigned to constant and temperature-dependent parameters in the model. Nitrogen was assumed to be the growth rate limiting substrate. Phytoplankton were assumed to excrete 30% of the inorganic nitrogen they took up based on the studies of *Bronk et al.* [1994] and *Bronk and Ward* [1999]. The gross growth efficiencies of the flagellates and ciliates were assumed to be 35% based on the work of *Fenchel and Finlay* [1983] and *Straile* [1997]. The filter feeders and carnivores were assigned gross growth efficiencies of 30% and 35%, respectively [*Raymont*, 1983; *Lalli and Parsons*, 1993; *Straile*, 1997]. The growth efficiencies with respect to carbon of heterotrophic marine bacteria in nature have been estimated to lie somewhere between a low of 5-10% [*Linley and Newell*, 1984; *Kirchman et al.*, 1991] and a high of 20-35% [*Bjornsen*, 1986; *Tranvik*, 1988; *Middleboe and Søndergaard*, 1993; *Carlson and Ducklow*, 1996]. The q_B for nitrogen may be much higher. As noted by *Goldman et al.* [1987, p. 1239] "Considering that amino acids frequently do not provide all the N required and that carbohydrates often are

Table 2. Values Assigned to Constant and Temperature-Dependent Parameters in the Model

Parameter	Value
q_{2S}	0.7
q_{2L}	0.7
q_3	0.35
q_4	0.35
q_5	0.3
q_6	0.35
q_B	1.00
r_{2S}	0.0
r_{2L}	0.0
r_3	0.3
r_4	0.3
r_5	0.3
r_6	0.5
A_{2S}	$(1.2/q_{2S})\exp(0.0633(T-25))$
A_{2L}	$(1.2/q_{2L})\exp(0.0633(T-25))$
A_3	$(2.4/q_3)\exp(0.1(T-25))$
A_4	$(2.4/q_4)\exp(0.1(T-25))$
A_5	$0.5\exp(0.1(T-25))$
A_6	$0.5\exp(0.1(T-25))$
A_B	$(1.2/q_B)\exp(0.0633(T-25))$
P_{2S}	7.5 nM
P_{2L}	75 nM
P_B	7.5 nM

Dimensions of A_m are d^{-1}. T is temperature in degrees C.

the major C source for growth of marine bacteria, . . . actively growing marine bacteria may be inefficient remineralizers of N." Accordingly, we assigned q_B a value of 1.0.

Phytoplankton were assumed to respire none of the inorganic nitrogen they took up, and as noted heterotrophic bacteria were assumed to convert dissolved organic nitrogen (DON) to biomass with 100% efficiency. The flagellates, ciliates, filter feeders, and carnivores were assumed to respire 30, 30, 30, and 50%, respectively, of the nitrogen they consumed [*Raymont*, 1983; *Lalli and Parsons*, 1993].

The temperature dependence of the nutrient-saturated phytoplankton growth rates was taken from *Eppley* [1972]. The model assumes that under nutrient-saturated conditions both the small and large phytoplankton are capable of growing at an average rate of 1.2 d^{-1} within the euphotic zone at a temperature of 25°C. This assumption is consistent with growth rates reported from field work in the subtropical gyres and equatorial Pacific [*Laws et al.*, 1984, 1987; *Latasa et al.*, 1997]. The substrate-saturated heterotrophic bacterial growth rates were assumed to follow the same pattern as the nutrient-saturated phytoplankton growth rates. This assumption is based in part on heterotrophic bacterial growth rates reported from field studies, which differ little from phytoplankton growth rates reported under similar conditions [*White et al.*, 1991]. Reported Q_{10} values for heterotrophic bacterial growth rates range between ~2-4 [*Hobbie and Cole*, 1984; *White et al.*, 1991] and are positively correlated with chlorophyll *a* (chl *a*) concentrations [*White et al.*, 1991]. The assumed Q_{10} for heterotrophic bacterial growth rates is 1.9 and gives growth rates of 0.25 d^{-1} at 0°C, comparable to values reported from estuarine and coastal habitats at that temperature [*White et al.*, 1991]. The maximum growth rates of the flagellates and ciliates was assumed to be 2.4 d^{-1} at 25°C based on studies by *Fenchel and Finlay* [1983]. The temperature dependence of those rates was assumed to be identical to that of copepods [*Huntley and Lopez*, 1992]. The maximum ingestion rates of the filter feeders and carnivores were assumed to be 0.5 d^{-1} at 25°C. This assumption gives maximum growth rates for the filter feeders and carnivores of 0.15 and 0.174 d^{-1}, within the range of values summarized from physiological rate measurements on copepods (0.14-0.39 d^{-1}) by *Huntley and Lopez* [1992] at 25°C. The temperature dependence of these rates was taken from *Huntley and Lopez* [1992].

P_{2S} and P_{2L} values were set at 7.5 and 75 nM, respectively. The latter is based on chemostat studies with the diatoms *Phaeodactylum tricornutum* and *Thalassiosira oceanica* [E. A. Laws, unpublished data 1998]. The former is a rough estimate and is based on studies by D. M. Karl [personal communication, 1999] at station ALOHA and *Holmes et al.* [2000] in the Sargasso Sea. P_b was assumed to be numerically identical to P_{2S}.

The assumption that the ciliates graze the small phytoplankton and heterotrophic bacteria in proportion to $X_{2S}/(X_B + X_{2S})$ and $X_B/(X_B + X_{2S})$, respectively, (Equations (2) and (10)) requires that the growth rates of the small phytoplankton and heterotrophic bacteria be identical in the steady state. This follows from the fact that the right-hand sides of (2) and (10) can be written in the forms $[\mu_{2S} - F_3/(X_B + X_{2S})]X_{2S}$ and $[\mu_B - F_3/(X_B + X_{2S})]X_B$, respectively, where μ_{2S} and μ_B are the growth rates of the small phytoplankton and heterotrophic bacteria, respectively. Mathematically this condition requires that $f_B q_B A_B = f_{2S} q_{2S} A_{2S}$. Likewise, (3) and (5) combined with the assumption of steady state require that the growth rates of the large phytoplankton and ciliates be identical, i.e., $f_{2L} q_{2L} A_{2L} = f_4 q_4 A_4$. Finally, the steady state assumption implies that $M = q_6 A_6 f_6$.

We assumed the system to adjust to the external loading rate L in a manner that produced a stable steady state as defined by *May* [1974]. May's definition of stability implies that the system is stable to small perturbations of the X_m from their equilibrium values. This is a reasonable requirement, since there is little point in discussing the characteristics of a steady state if the steady state is not stable to small perturbations. In order to obtain a unique solution to the equations, we further required that the steady state solution be more stable to small perturbations than any other steady state solution. This is an arbitrary assumption, and there is no a priori reason to believe that pelagic ecosystems evolve toward a condition of maximum stability. Mathematically, a steady state is stable to small perturbations if the real parts of all the eigenvalues of its community matrix are negative [*May*, 1974]. The community matrix for (1)-(10) is a 10x10 matrix consisting of the partial derivatives of the right-hand sides of (1)-(10) with respect to the X_m, evaluated at the equilibrium point. For example, the element in the 1st row and 2nd column of the community matrix is the partial derivative of equation 1 with respect to the second state variable, X_{2S}. Requiring that the system has maximum stability implies that the least negative eigenvalue associated with a given steady state be more negative than the least negative eigenvalue of any other steady state.

For each combination of external loading rate and temperature, the parameters f_{2L}, f_3, f_5, f_6, and X_5 were chosen so as to produce a steady state with maximum stability. Given f_{2L}, X_1 is equated to $P_{2L}/(1 - f_{2L})$ and $f_{2S} = 1 - P_{2S}/X_1$. Given f_{2S} and f_{2L}, f_B is equated to $q_{2S}A_{2S}f_{2S}/(q_B A_B)$, and f_4 to $q_{2L}A_{2L}f_{2L}/(q_4 A_4)$. Given f_B, the concentration of DON is equated to $P_B/(1 - f_B)$. Particulate organic nitrogen (PON) is equated to L/D. At this point X_{2S}, X_{2L}, X_3, X_4, X_6, and X_B can be determined if f_3, f_5, f_6, and X_5 are specified. Specification of f_3, f_5, and f_6 is equivalent to specifying P_2, P_5, and P_6. In effect one assumes that the compositions of the flagellate, filter feeder, and carnivore communities adjust themselves in response to changes in their food supply. In the case of the phytoplankton trophic level, this adjustment is achieved by changes in the relative proportions of small and large phytoplankton. Specifying X_5 is a form of top-down control. The total biomass of filter feeders is assumed to change in a way that maximizes the stability of the steady state.

With a little algebraic manipulation, it is straightforward to show that the equilibrium values of X_{2S}, X_{2L}, X_3, X_4, X_6, and X_B solve the following set of linear equations:

$$q_{2L}A_{2L}f_{2L}(X_{2L} + X_4) = A_5X_5f_5 \tag{12}$$

$$q_{2S}A_{2S}f_{2S}(X_{2S} + X_B) - A_3f_3X_3 = 0 \tag{13}$$

$$(s_{2L}A_{2L}f_{2L} + q_{2L}A_{2L}f_{2L}(s_5 + q_5(1 - r_6)))X_{2L} + q_{2L}A_{2L}f_{2L}(s_5 + q_5(1 - r_6))X_4 = L \tag{14}$$

$$q_3A_3f_3X_3 - A_4f_4X_4 = 0 \tag{15}$$

$$s_{2S}A_{2S}f_{2S}X_{2S} + (s_3 + s_4q_3)A_3f_3X_3 - A_Bf_BX_B = 0 \quad (16)$$

$$q_5q_{2L}A_{2L}f_{2L}(X_{2L} + X_4) - A_6f_6X_6 = 0 \quad (17)$$

These equations are independent of D. Hence, with the exception of the concentration of detrital PON, none of the state variables is a function of D. Logically $D = S/Z$, where S is the sinking rate of the PON and Z is the depth of the euphotic zone. Because (12)-(17) are independent of D, with the exception of PON, none of the X_m depends on the assumed sinking rate of the PON. The initial procedure for determining the most stable configuration of the system at a given loading rate was to vary f_{2L}, f_3, f_5, f_6, and X_5 over a range of values and to determine the combination that produced the most stable steady state. The grid search for f_{2L}, f_3, f_5, and f_6 was very straightforward, since all these parameters are dimensionless and must lie in the range [0, 1]. Not surprisingly, the optimum value of X_5 was highly correlated with the external nutrient-loading rate. After exploring a wide range of conditions, we discovered that the optimum values of f_{2L}, f_3, f_5, and f_6 were highly correlated with one another and that there was little to be gained by treating them as independent variables. The optimum values were related as follows:

$$f_3 = \frac{f_{2L}}{3} \quad (18)$$

$$f_5 = \frac{0.13 + 1.52f_{2L}}{0.65 + f_{2L}} \quad (19)$$

$$f_6 = 0.6f_5 \ . \quad (20)$$

Using (18)-(20) we were able to reduce the problem of finding the optimum steady state configuration to a two-dimensional grid search involving f_{2L} and X_5. In effect this amounts to optimizing the system through bottom-up (f_{2L}) and top-down (X_5) control.

3. Results

The results of the modeling exercise are shown in Figures 1-6, Plates 1-6, and Tables 3-5. Because the system was assumed to be in steady state, export production and new production are identical. Under such conditions, there is no reason to distinguish between e and f ratios, and we will henceforth refer to such ratios as ef ratios. For purposes of determining steady state solutions, it was mathematically convenient to treat temperature (T) and external loading rate (L) as the independent variables in the model. The ef ratio calculated from the steady state solutions may therefore be regarded as a function of T and L, i.e., ef = $F(T, L)$. However, because NP = L/ef, it follows that

$$\text{ef} = F(T, (\text{NP})(\text{ef})) \ . \quad (21)$$

Equation (21) defines a relationship between T, NP, and the ef ratio. Because NP can be estimated from satellite data and is commonly measured in field studies, we have chosen to present our calculated ef ratios as a function of T and NP rather than T and L.

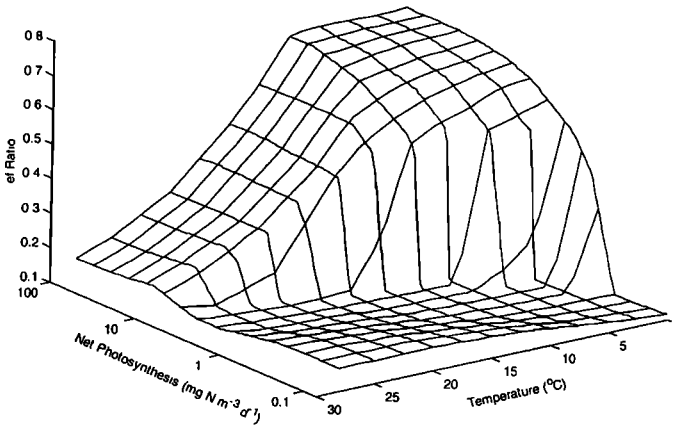

Figure 2. Calculated ef ratios as a function of temperature and net photosynthetic rate.

Figure 2 shows the ef ratios that maximized system stability as a function of temperature and NP. At temperatures of 25°-28°C the ef ratio is relatively insensitive to total production and consistently lies in the range 0.1-0.2. At lower temperatures there is a transition between a region of low ef ratios at low rates of production to high ef ratios at high rates of production. The high ef ratios are strongly temperature dependent. At temperatures of 0°-10°C the highest ef ratios are ~0.67. However, there is a very steep drop in the maximum ef ratio between temperatures of 10° and 20°C. At 20°C the maximum ef ratio is ~0.3.

In Figure 3 we have compared the results of the model with data obtained during the JGOFS process and time series studies. In each case the inputs to the model were the total areal production rate and the temperature and depth of the euphotic zone. We have also included results reported from the North Pacific subarctic gyre (Station P) by *Wong et al.* [1998], from the northeast water (Greenland) polynya by *Smith* [1995] and *Smith et al.* [1997], and from the Peruvian upwelling system by *Wilkerson et al.* [1987]. The methodologies used to estimate new/export production and total production are summarized in Table 3. In most cases, total production in terms of nitrogen was equated to net photosynthesis as estimated by 24-h ^{14}C uptake experiments divided by the Redfield C:N ratio of 5.7 by weight. In some cases, gross production estimates based on ^{18}O tracer studies were also available, but it would have been necessary to multiply the gross production numbers by a conversion factor to obtain estimates of net photosynthesis [*Laws et al.*, 2000]. For purposes of internal consistency, we elected to base our calculations on the ^{14}C data. The one exception was the Greenland polynya study, where we estimated new and total production strictly from ^{15}N tracer results. We made an exception in this case because the reported ^{14}C results were corrected for ice cover and the ^{15}N results were not. Since *Smith* [1995] and *Smith et al.* [1997] estimated ef ratios on the basis of their ^{15}N data and since carbon synthesis, nitrate uptake, and ammonium uptake respond differently to light limitation, we felt it best to restrict our analysis to the ^{15}N results in this case.

There is no consensus on the best way to estimate new/export production. Traditional estimates of new production based on nitrate uptake may be misleading if the additions of ^{15}N-labeled

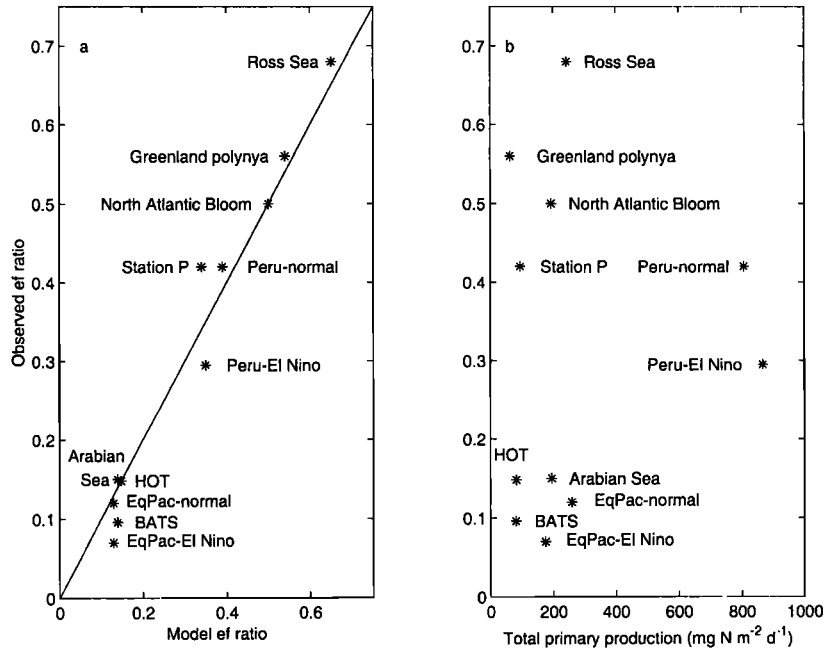

Figure 3. (a) Model ef ratio versus observed ef ratios at locations in Table 3. The straight line is the 1:1 line. (b) Total primary production versus observed ef ratios at the locations in Table 3.

Table 3. Field Data and Methods of Analysis

Area	Z_m	Temperature °C	Export or New Production	Method of Calculation	Total Production	Method of Calculation
BATS	140	21	7.8	carbon balance assuming Redfield C:N [*Michaels et al.*, 1994]	82	^{14}C production from *Michaels et al.* [1994] divided by Redfield C:N
HOT	150	25	12.2	average of O_2 and C mass balances, assuming Redfield ratios [*Emerson et al.*, 1997]	83	^{14}C production from *Karl et al.* [1996] divided by Redfield C:N
NABE	35	12.5	98	total production times mean f ratio of *Bender et al.* [1992] and *McGillicuddy et al.* [1995]	194	^{14}C production from *Buesseler et al.* [1992] divided by Redfield C:N
EqPac-normal	120	24	32.1	total production times f ratio from *Landry et al.*, [1997] based on ^{15}N uptake ratios	260	^{14}C production from *Landry et al.* [1997] divided by Redfield C:N
EqPac-El Niño	120	27	12.3	total production times f ratio of *Landry et al.* [1997] based on ^{15}N uptake ratios	169	^{14}C production from *Landry et al.* [1997] divided by Redfield C:N
Arabian Sea	65	25	29.2	total production times f ratio of *McCarthy et al.* [1999] based on ^{15}N uptake ratios	195	^{14}C production from *Buesseler et al.* [1998] divided by Redfield C:N
Ross Sea	40	0	165	total production times f ratio of *Asper and Smith* [1999] from ^{15}N uptake ratios	243	^{14}C production from *Asper and Smith* [1999] divided by Redfield C:N
Subarctic Pacific-Station P	120	6	40.3	mean nitrate uptake/utilization from *Sambrotto and Lorenzen* [1987], *Emerson et al.* [1993], and *Wong et al.* [1998]	95	mean ^{14}C production from *Welschmeyer et al.* [1991] and *Wong et al.* [1995] divided by Redfield C:N
Peru-normal	25.5	16.8	339	Nitrate uptake using ^{15}N tracer [*Wilkerson et al.*, 1987]	806	^{14}C production from *Wilkerson et al.* [1987] divided by Redfield C:N
Peru-El Niño	17.8	17.4	256	nitrate uptake using ^{15}N tracer [*Wilkerson et al.*, 1987]	867	^{14}C production from *Wilkerson et al.* [1987] divided by Redfield C:N
Greenland polynya	50	0	35.6	nitrate uptake using ^{15}N tracer [*Smith*, 1995; *Smith et al.*, 1997]	63.2	^{15}N uptake from *Smith* [1995] and *Smith et al.* [1997]

Units of production are mg N m^{-2} d^{-1}.

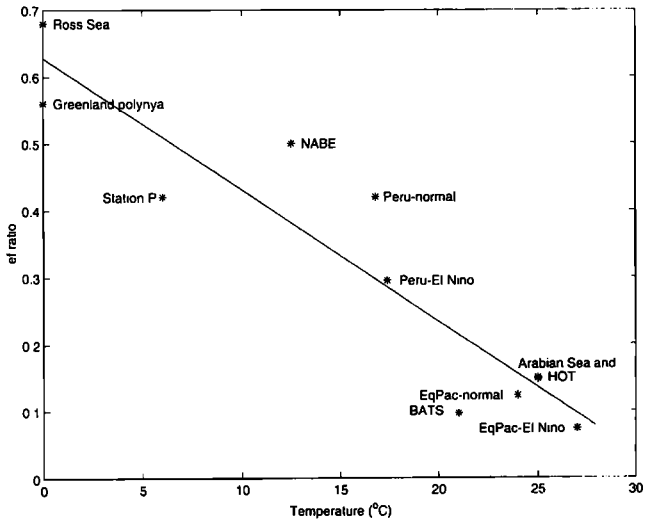

Figure 4. Temperature versus observed ef ratio at locations in Table 3. The straight line is a model I least squares regression line; $r^2 = 0.86$.

substrates perturb ambient concentrations [*Allen et al.*, 1996] or if a significant amount of nitrification occurs within the euphotic zone [*Dore and Karl*, 1996]. Export production has often been estimated from the downward flux of particulate material, but other processess may contribute significantly to the export of organic matter in some cases [*Michaels et al.*, 1994]. Careful mass balance calculations may provide the best estimates of new/export production, and we relied on such mass balance calculations at the BATS and HOT sites. At the remaining stations we estimated new production from nitrate uptake/assimilation based either on changes in nitrate concentrations or uptake of ^{15}N-labeled substrates.

The agreement between the observed ef ratios and the ratios predicted by the model for the given temperature and rate of total production is excellent. The importance of temperature is dramatically illustrated by a comparison of Figures 3a and 3b. There is no significant correlation between the observed ef ratios and total production. In fact, temperature alone can account for 86% of the variance in the observed ef ratios (Figure 4). However, the ratios are a function of more than temperature. The ratios at Station P and off the coast of Peru during normal upwelling conditions are virtually identical, but the temperature at Station P is more than 11°C cooler than the temperature in the Peruvian upwelling system. The explanation for the similarity of the ratios is the much higher rate of primary production in the Peruvian upwelling system.

Figure 5a shows steady state values of phytoplankton carbon calculated by the model versus observed concentrations of chl *a*. Almost all the data lie within the curves corresponding to C:chl *a* ratios of 20 and 150 by weight, and there is a clear tendency for the ratios to be higher at low temperatures. A negative correlation between C:chl *a* ratios and temperature has been observed experimentally [*Eppley*, 1972] and is predicted by theoretical models [*Shuter*, 1979]. The rationale is that the dark reactions of photosynthesis involve many temperature-sensitive enzymatic reactions and that the light reactions of photosynthesis are relatively temperature insensitive. Other things being equal, cells must allocate a higher percentage of their cellular carbon to the dark reactions of photosynthesis and a smaller percentage to the light reactions to achieve balanced growth at low temperatures. The data in Fig. 5a are consistent with this expectation, and the implied C:chl *a* ratios fall within the range of values reported in the literature [*Campbell et al.*, 1994; *DeJonge*, 1980; *Eppley*, 1968, 1972; *Eppley et al.*, 1971, 1977; *Hunter and Laws*, 1981; *Jones et al.*, 1996; *Laws et al.*, 1984; *Parsons et al.*, 1961; *Steele and Baird*, 1962]. At the low end of the temperature spectrum, phytoplankton C:chl a ratios have been estimated in the Ross Sea/Southern Ocean by *Sakshaug and Holm-Hansen* [1986], *DiTullio and Smith* [1996], and *Smith et al.* [1996]. Their estimates average 126 ± 28 by weight. The ratio predicted by the model is 123 (Table 4). Toward the high end of the temperature spectrum, *Karl and Dobbs* [1998] estimate autotrophic biomass to be 2.78 mg C m^{-3} in the upper 150 m at station ALOHA. This biomass is virtually identical to the model estimate (Table 4) and gives a C:chl a ratio of 18.5 by weight.

Figure 5b shows the ratio of heterotrophic bacterial carbon to phytoplankton carbon estimated by the model versus temperature at the 11 locations in Table 3. Bacterial carbon was calculated assuming a bacterial C:N ratio of 4.8 by weight [*Goldman et al.*, 1987]. At temperatures greater than roughly 20°C the model predicts that heterotrophic bacterial carbon exceeds autotrophic microbial carbon by ~20%. Below 20°C, there is a distinctly positive correlation between the ratio of heterotrophic/autotrophic microbial carbon and temperature. At a temperature of 0°C the autotrophic microbial carbon exceeds the heterotrophic microbial carbon by more than a factor of 50. The trends apparent in Fig. 5b are similar to patterns of heterotrophic bacterial abundance in ocean surface waters described by *Li* [1998]. Figure 6 compares estimates of heterotrophic bacterial carbon from the model versus field data. The model accounts for more than 99% of the variance in the field data.

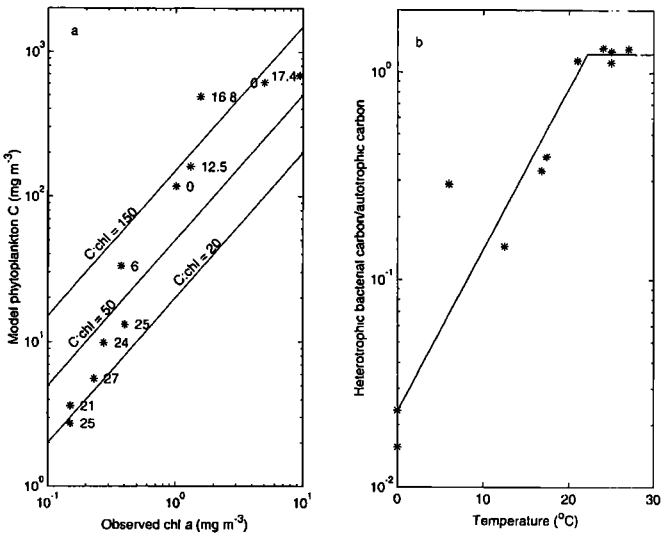

Figure 5. (a) Observed chl *a* concentrations versus model autotrophic carbon concentrations for locations in Table 3. Numbers next to symbols indicate temperatures of environment from Table 3. (b) Temperature versus ratio of model heterotrophic bacterial carbon to autotrophic carbon concentration for locations in Table 3.

Table 4. Observed and Calculated Parameters at Locations in Table 3

Location	$f_{observed}$	f_{calc}	Observed chl *a* (mg m^{-3})	Model Autotrophic C (mg m^{-3})	Model Bacterial C (mg m^{-3})
BATS	0.10	0.14	0.15	3.62	4.14
HOT	0.15	0.15	0.15	2.74	3.07
NABE	0.51	0.51	1.31	160	23.1
EqPac-normal	0.12	0.13	0.28	9.88	13.0
EqPac-El Nino	0.07	0.13	0.23	5.60	7.3
Arabian Sea	0.15	0.14	0.40	13.2	16.7
Ross Sea	0.68	0.65	5.0	613	9.6
Station P	0.42	0.34	0.38	33	9.5
Peru-normal	0.42	0.39	1.6	487	163
Peru-El Niño	0.30	0.35	9.4	685	268
Greenland	0.56	0.54	1.0	115	2.7

In order to examine the implications of the model with respect to global export production, we calculated net primary production (NPP) with the vertically generalized production model of *Behrenfeld and Falkowski* [1997a] using SeaWiFS ocean color data for the 12-month period beginning October 1997 and NASA's derived global chlorophyll fields. The average daily NPP for each month was used to obtain a global annual map of NPP. The calculated global NPP for the 12-month period was 52.1 Gt of carbon. Sea surface temperature (SST) fields were derived from monthly advanced very high resolution radiometer (AVHRR) global data. Export production was calculated for each month using three different algorithms: (1) the Eppley-Peterson model (EP model), the temperature-export ratio regression in Figure 4 (TE model), and the model presented here (Figure 2), which relates export ratios to net primary production and temperature (PTE model). In the case of the PTE model, ef ratios were derived from a look-up table generated from the interpolated values shown in Figure 2. In the case of both the TE and PTE models, we assumed, to first order, that the temperature in the euphotic zone was equal to the SST and that nitrogen-based total production values were related to carbon equivalents by the Redfield C:N ratio of 5.7 by weight. Annual average ef ratios were calculated from the ratio of annual export production to NPP. The results of this exercise are summarized in Table 5 and Plates 1-6.

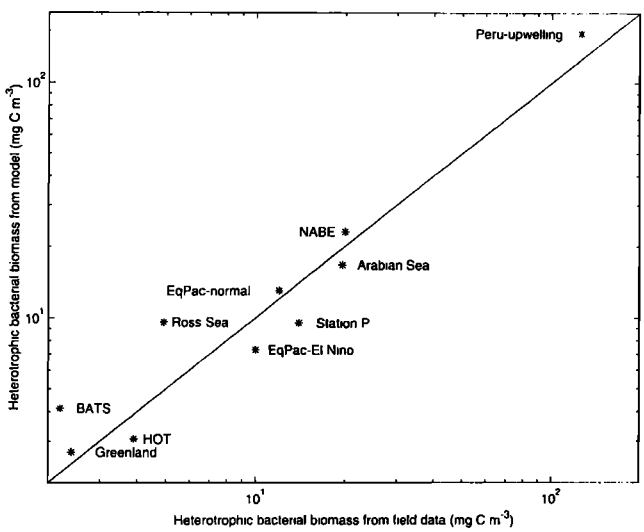

Figure 6. Relationship between estimates of heterotrophic bacterial carbon from the model and from field data. Sources of field data are as follows: Ross Sea and BATS [*Carlson et al.*, 1998], HOT [*Karl and Dobbs*, 1998], Station P [*Kirchman et al.*, 1993], EqPac [*Ducklow et al.*, 1995], NABE [*Ducklow et al.*, 1993], Arabian Sea [*Ducklow et al.*, 2000], Greenland [*Yager*, 1996], Peru-upwelling [*Sorokin and Kogelschatz*, 1979, median at stations with chl *a* concentrations > 1 mg m^{-3}, assuming 120 fg C μm^{-3} (*Carlson et al.*, 1998)].

Export ratios generated by the EP model of course tracked NPP and were highest in coastal and upwelling areas. Not surprisingly, average ef ratios generated by the TE model increased monotonically with latitude. On the basis of current understanding, they are unrealistically low for many tropical and temperate coastal and continental shelf ecosystems. At high latitudes they are much higher than the ef ratios calculated using the EP and PTE models. The PTE model produced ef ratios that were low in tropical and subtropical latitudes and highest in relatively shallow northern temperate and polar seas and in the Antarctic Ross and Weddell Seas. The global average ef ratio predicted by the PTE model, 0.21, is only a little more than half the ef ratio estimated using the EP model. The difference is primarily a consequence of the behavior of the two models in the low latitude gyres (Table 5).

Global export production is similar when estimated using the TE and PTE models. The only significant difference in export production estimated using the TE and PTE models occurs in the Southern Ocean, where the export estimated by the TE model is about twice the value estimated using the PTE model. The ef ratio of 0.58 calculated for the Southern Ocean using the TE model seems unrealistically high considering the work of *Huntley et al.* [1991, p. 64], who concluded "An analysis of the food web for these waters implies that the Southern Ocean may be remarkably inefficient as a carbon sink." Although new production may account for roughly 2/3 of NPP during bloom events (Table 4), the low production that prevails during much of the year in the Antarctic Ocean appears to be associated with little accumulation of biomass or drawdown of CO_2 [*Smetacek et al.*, 1997]. This conclusion is consistent with the PTE model.

Estimates of export production calculated using the EP, TE, and PTE models may be compared to calculations of new

Table 5. Export production and ef ratios calculated using the EP, TE, and PTE models

	EP		TE		PTE	
	Export	ef	Export	ef	Export	ef
Ocean Basin						
Pacific	8.3	0.37	4.9	0.22	4.3	0.19
Atlantic	7.4	0.42	4.4	0.25	4.3	0.25
Indian	4.3	0.42	1.9	0.18	1.5	0.15
Antarctic	0.69	0.31	1.3	0.58	0.62	0.28
Arctic	0.12	0.44	0.15	0.56	0.15	0.56
Mediterranean	0.36	0.46	0.21	0.27	0.19	0.24
Global	20.9	0.39	12.9	0.24	11.1	0.21
Total Production						
Oligotrophic (chl $a < 0.1$ mg m^{-3})	1.9	0.27	1.02	0.15	1.04	0.15
Mesotrophic ($0.1 \leq$ chl $a < 1.0$ mg m^{-3})	14.0	0.38	9.09	0.25	6.5	0.18
Eutrophic (chl $a \geq 1.0$ mg m^{-3})	4.96	0.49	2.73	0.27	3.6	0.36
Ocean Depth						
0-100 m	3.4	0.49	1.6	0.23	2.2	0.31
100 m -1 km	1.9	0.45	1.2	0.28	1.4	0.33
> 1 km	15	0.36	9.9	0.24	7.4	0.18

Units of export are Gt C yr^{-1}.

production based on seasonal fluxes of oxygen between the ocean and atmosphere. Assuming a molar O_2:C ratio of 1.45, *Najjar and Keeling* [2000] have estimated new production at latitudes higher than 20° to be ~5 Gt C yr^{-1}. Comparable values calculated using the EP, TE, and PTE models are 14, 11, and 8 Gt C yr^{-1}, respectively. Considering the various sources of error, there is probably no significant difference in the export production estimate obtained by *Najjar and Keeling* [2000] and the PTE model.

4. Discussion

Although derived from the output of a food web model, the PTE model may to some extent be regarded as a hybrid of the EP and TE models, both of which are based on empirical relationships derived from field data. The EP and TE models consider the ef ratio to be solely a function of net photosynthetic rate and temperature, respectively. The results of the PTE model suggest that information on both NPP and temperature are needed to explain the temporal and spatial variability of ef ratios.

Qualitatively the temperature effect is easy to understand. At high temperatures the potential growth rates of microorganisms are high, and most organic matter is decomposed before it has a chance to leave the euphotic zone. At cold temperatures the potential growth rates of heterotrophic organisms are much lower, and at moderate to high rates of primary production, much of the organic matter produced in the euphotic zone is exported before it has a chance to decompose. In effect, the autotrophic community is nutrient limited, and the heterotrophic community is temperature limited. At moderate to high loading rates the extent of nutrient limitation of the autotrophic community is much less than the degree of temperature limitation of the heterotrophic community. The result is a surplus production of organic matter that is exported from the system. As the external nutrient loading rate is reduced, the extent of nutrient limitation of the autotrophic community increases and the heterotrophic community catabolizes a greater percentage of the organic matter produced by the autotrophs. The transition between relatively high and low ef ratios logically occurs at progressively lower loading rates as the temperature of the system decreases.

In several previous papers relationships between temperature and nitrate concentration have been used in empirical models to estimate new production in the northwest African upwelling system and on Georges Bank [*Dugdale et al.*,1989; *Sathyendranath et al.*, 1991]. Such models have utility on a regional scale, but there is no global relationship between nitrate concentrations and f ratios. In the model developed here, the impact of temperature on ef ratios is associated with the assumed temperature dependence of microbial growth rates. The success of the model in describing ef ratios in a wide variety of habitats (Figure 3a) suggests that incorporating temperature effects in this way may take account of one of the more fundamental influences of temperature on the behavior of pelagic food webs.

The sharpness of the transition between high and low ef ratios may be an artifact of the requirement that system stability be maximized. At the transition point, two system configurations have very similar least negative eigenvalues. The eutrophic configuration corresponds to a relatively high ef ratio; the oligotrophic configuration corresponds to a low ef ratio of ~0.1. Since the least negative eigenvalues of the two configurations are so similar at the transition point, there is little reason to prefer one configuration over the other from the standpoint of system stability. The transition between the high and low ef ratio modes may therefore be more gradual than is implied in Figure 2.

Although our model was formulated to describe the characteristics of steady state food webs, it appears to give remarkably good estimates of ef ratios in cases where production and/or biomass change rapidly, for example, spring blooms and upwelling systems. Several considerations may explain the ability of the model to provide good estimates of ef ratios for non-steady state systems. First, temperature will influence the

rate of decomposition of organic matter in a qualitatively similar way, regardless of whether a system is at steady state or not. Second, because of the short generation time of microorganisms, large changes in planktonic biomass and production may occur over a timescale of several weeks under conditions where there is only a small imbalance between production and consumption. As noted by *Hutchinson* [1967, p. 376], the seasonal cycle of planktonic organisms over the course of a year is equivalent to as many as 10,000 years in the successional history of a forest. In other words, what appear from the human perspective to be rapid changes in the biomass and production of planktonic communities are much more gradual when scaled to the division times of microorganisms.

Since the seminal paper by *Eppley and Peterson* [1979], there has been a general consensus that an approximately hyperbolic relationship existed between ef ratios and total production. Figure 2 suggests that such a hyperbolic relationship is part of a more complex pattern. At temperatures less than ~25°C there is a positive correlation between ef ratios and total production when the full range of the latter is considered. However, this pattern is due entirely to the transition between low and high ef ratios at intermediate levels of production. When the low ef ratio modes are considered separately, there is actually a gradual decrease of ef ratios with increasing total production. The level of noise in most field data would make such a small slope statistically insignificant in the absence of a large data set. We are aware of only one study [*Karl et al.*, 1996] where such a negative correlation has been demonstrated between ef ratios and total production in an oligotrophic system. In that case the correlation was documented using data collected on a monthly basis for a period of 3 years (1990-1992) at station ALOHA.

The explanation for the negative correlation between production and ef ratios under oligotrophic conditions is related to the fact that under oligotrophic conditions the large phytoplankton are the weak link in the food web. A perturbation to the large phytoplankton is potentially very destabilizing because $P_{2L} >> P_{2S}$. To maintain system stability as allochthonous nutrient inputs are reduced, more grazing pressure is applied to the small phytoplankton, and the percentage of nutrients allocated to the large phytoplankton increases by a small amount. This causes the ef ratio to increase. Analogues of this strategy exist in multispecies fisheries management [*May et al.*, 1979].

A similar explanation underlies the positive correlation between ef ratios and temperature under oligotrophic conditions. Since nutrient-saturated growth rates are assumed to be positively correlated with temperature, increasing temperature tends to reduce relative growth rates sensu *Goldman* [1980], that is, the growth rates as a percentage of their nutrient-saturated values become smaller. As relative growth rates decrease, maximum system stability is again achieved by routing a greater percentage of nutrients to the large phytoplankton, since under oligotrophic conditions the large phytoplankton are the weak link in the system. Under eutrophic conditions the ambient nutrient concentration is much greater than P_{2L}. The large phytoplankton are no longer so susceptible to perturbations of the limiting nutrient concentration, and other considerations determine the system configuration of maximum stability.

Although the model accounts for over 97% of the variance in the observed ef ratios (Figure 3a), temperature alone accounts for 86% of the variance. The ability of temperature to account for so much of the variance in ef ratios is due to two factors. First, at temperatures ≥ 25°C, ef ratios are low at all rates of production. Second, at moderate to high rates of production, there is a distinctly negative correlation between temperature and ef ratios, and the latter are relatively insensitive to the rate of total production. According to the model, ef ratios are sensitive to both temperature and production only at low to moderate rates of production and at temperatures less than ~25°C. Because low surface water temperatures tend to promote vertical mixing, low temperatures are virtually never associated with low production in nutrient-limited systems. Low temperatures may, however, be associated with low production rates in light-limited systems, and this fact accounts for the tendency of the TE model to overestimate export production at high latitudes.

In addition to its ability to explain patterns in ef ratios, the PTE model provides estimates of autotrophic and heterotrophic microbial biomass that are consistent with field data. Chl *a* concentrations measured in the field combined with the model's estimate of autotrophic carbon yield C:chl *a* ratios that are consistent with values reported in the literature and imply a temperature dependence of the C:chl *a* ratio that is in accord with both empirical studies and theoretical understanding. The predicted estimates of heterotrophic bacterial carbon are in excellent agreement with field data from a wide spectrum of habitats (Figure 6).

Within the context of our model, the positive correlation between temperature and the ratio of heterotrophic to autotrophic microbial carbon (Figure 5b) is only indirectly due to temperature effects. High ef ratios imply that most organic matter is being routed through the large phytoplankton based food chain (Figure 1). Under these conditions, little DOM is produced to support heterotrophic bacterial growth. A corollary of this conclusion is that the carbon pools in polar systems tend to be particle dominated, in contrast to warm environments, where the microbial loop and DOM play a much greater role [*Carlson et al.*, 1998].

5. Sensitivity Analysis

Qualitatively the dependence of calculated ef ratios on production and temperature as depicted in Figure 2 is very insensitive to values assigned to the parameters in the model. The calculated ef ratios are positively correlated with assumed growth efficiencies. Reducing the animal Q_m values to 0.2-0.25, for example, reduces the calculated ef ratios by ~0.05-0.1. One of the most important parameters in the model is the heterotrophic bacterial growth efficiency, which we assumed to be 1.0. Reducing Q_B does not reduce the ef ratios dramatically, but it does have a significant effect on the calculated heterotrophic bacterial biomass. Had we assumed that Q_B was much less than 1, for example, 0.2, the calculated heterotrophic bacterial biomass would have been well below values reported from field studies. Our assumption that $Q_B = 1$ is consistent with *Goldman et al.*'s [1987, p. 1239] conclusion that "Actively growing bacteria may be inefficient remineralizers of N" and with earlier studies of *Johannes* [1965] and *Goldman and Caron* [1985], who concluded that protozoans were responsible for the bulk of nutrient regeneration and excretion in most parts of the ocean.

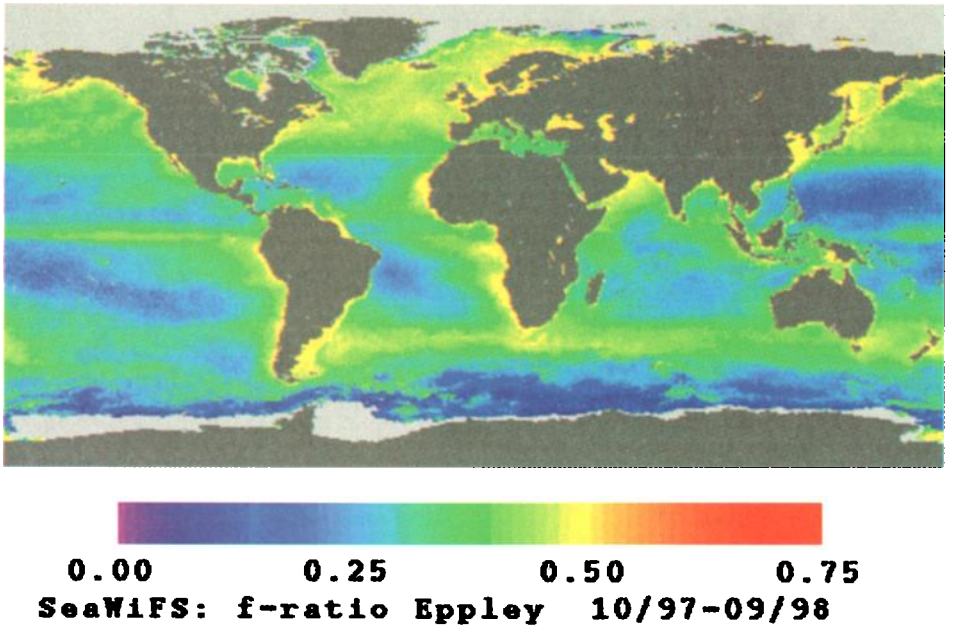

Plate 1. Annual average ef ratios calculated from the EP model. Net photosynthesis was estimated on a monthly basis as described in the text using data collected by the SeaWiFS satellite from October 1997 to September 1998.

One of the more uncertain parameters in the model is the temperature coefficient for heterotrophic bacterial growth. As noted, reported Q_{10} values for heterotrophic bacterial growth range between 2 and 4 [*Hobbie and Cole*, 1984; *White et al.*, 1991]. By assuming the temperature coefficient for autotrophs and heterotrophic bacteria to be identical, we effectively assigned the heterotrophic bacteria a Q_{10} of 1.9. In order to explore the implication of other possibilities, we reran the model with a Q_{10} of 4 for the heterotrophic bacteria, with the assumed A_B at 0°C the same as in the standard model. The ef values and other system properties at 28°C (the most extreme case) were virtually identical at high production rates with this change. The principal change occurred at low production rates, where ef ratios were higher than in the standard model by 0.05-0.10.

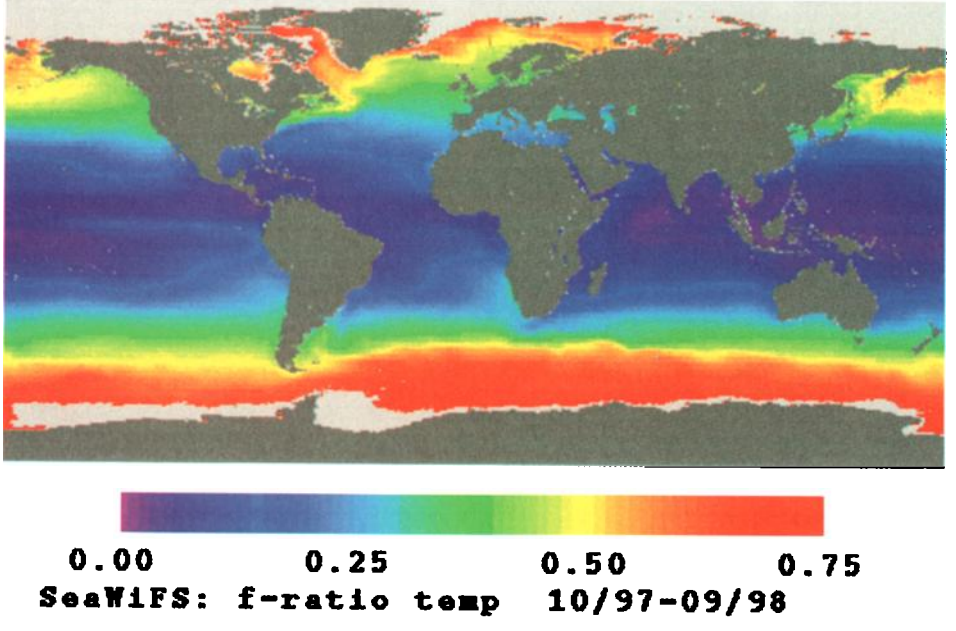

Plate 2. Annual average ef ratios calculated using the TE model Sea surface temperature (SST) fields were derived from monthly AVHRR global data as described in the text

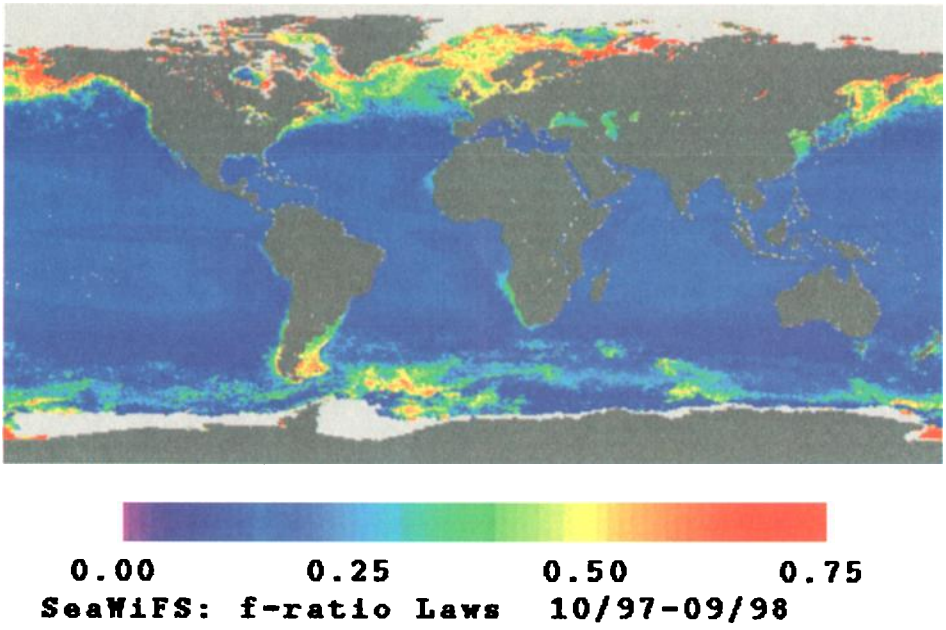

Plate 3. Annual average ef ratios calculated from the PTE model. Net photosynthesis and temperature were calculated as indicated in Plates 1-2.

6. Implications for Global Change

It is hoped that the results presented here will be of use to those modeling the larger scale impacts of climate change on the productivity of the oceans. On the basis of the results in Figure 2, warming the surface waters of the ocean would be expected to decrease ef ratios in the more productive parts of the ocean and particularly in the temperature range 10-20°C. In relatively warm oligotrophic regions, ef ratios might actually increase, but under any conditions the ef ratios in such regions would be low, i e , 0.10-0.15. An important concern is that warming of surface waters would restrict vertical circulation and reduce allochthonous nutrient inputs. Such a change might shift some systems across the transition from high to low ef ratio modes and dramatically reduce the export of organic carbon to the interior of the ocean.

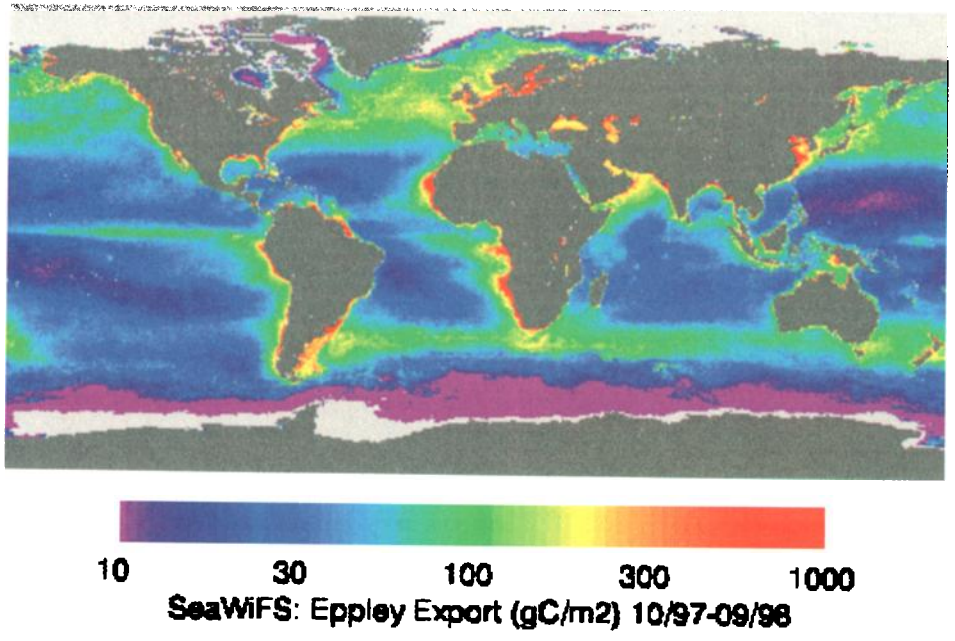

Plate 4. Annual export production calculated from the EP model and estimates of net photosynthesis as indicated in Plate 1

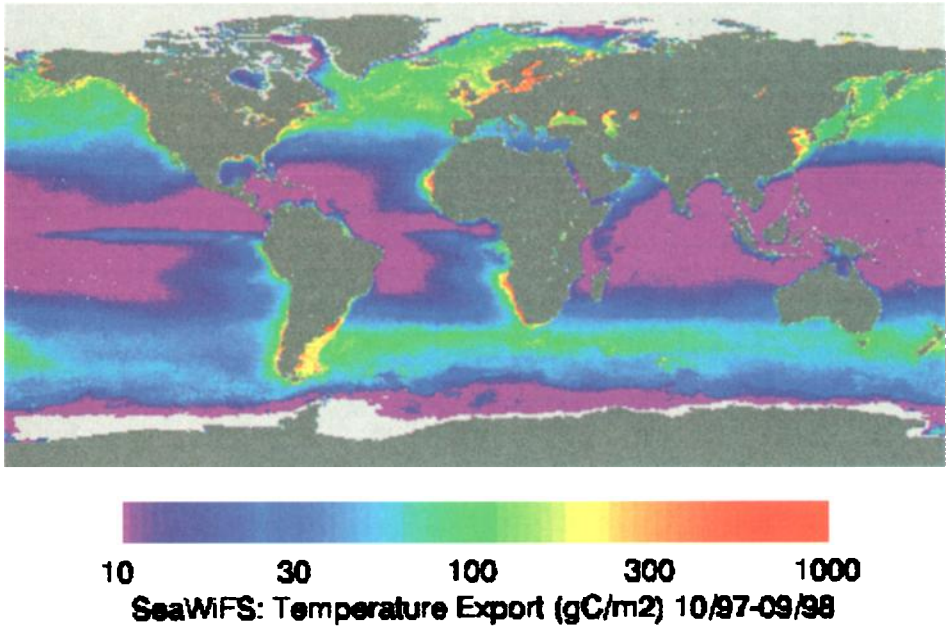

Plate 5. Annual export production calculated from the TE model and estimates of temperature and net photosynthesis as indicated in Plates 1 and 2.

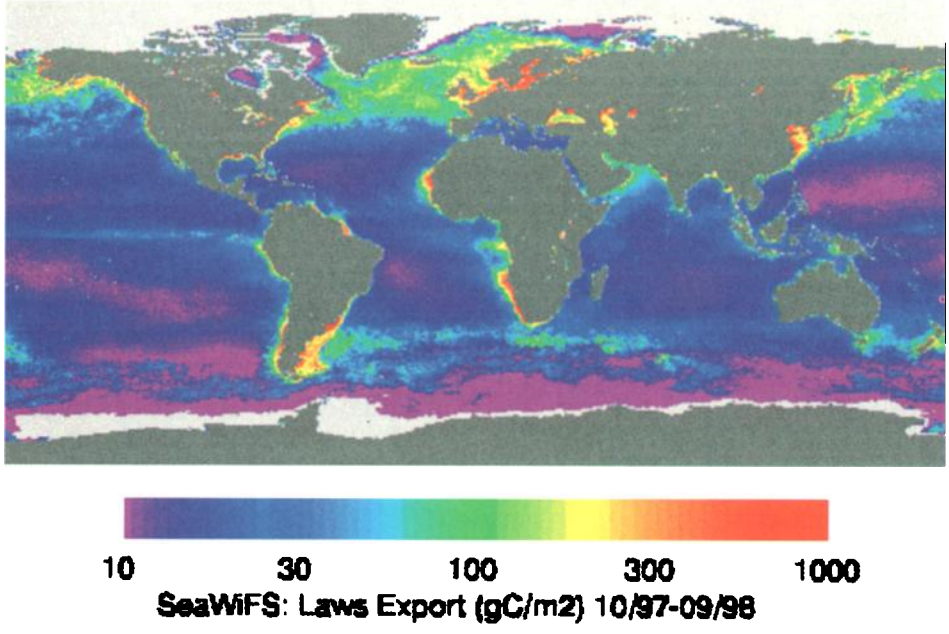

Plate 6. Annual export production calculated from the PTE model and estimates of temperature and net photosynthesis as indicated in Plates 1 and 2.

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H. Ducklow and W. O. Smith, Virginia Institute of Marine Sciences, College of William and Mary, Box 1346, Gloucester Point, VA 23062. (duck@vims.edu; wos@vims.edu)

P. G. Falkowski, Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901. (falko@imcs.rutgers.edu)

E. A. Laws, Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822. (laws@soest.hawaii.edu)

J. J. McCarthy, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138. (james_j_mccarthy@harvard.edu)

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